

Keiko KOSUGE* & Michio TAMURA*: **Ontogenetic studies
on petals of the Ranunculaceae**

小菅桂子*・田村道夫*: キンボウゲ科における花卉の発生

In the Ranunculaceae the petals are considered as modified stamens and called "Honigblätter" (Prantl 1887) or "Nectarblätter" (Janchen 1949), because they usually secrete nectar. They are cup-shaped, spurred or flat with a nectary at the bottom of cup or spur, or near the base of flat blade. The nectary is sometimes absent in some genera such as in *Anemonopsis* and *Adonis*. The petals vary greatly in this family; nevertheless, they seem to be made according to a planned scheme. Baum (1952) and Leinfellner (1958, 1959, 1964) considered that the petals in *Ranunculus* were peltate diplophyllous organs as well as stamens. Hiepko (1965) also thought that the petals in this family were basically peltate and changed to epeltate by the loss of nectar secretion. The petals have been studied by means of light microscopy (Payer 1857, Tepfer 1953, Hiepko 1965), but the developmental processes, especially in early stage, are insufficiently known. In order to understand the relationship between various types of petals in the Ranunculaceae we embarked on ontogenetic studies using electron microscopy.

Materials and methods Various stages of petal ontogeny were observed in 19 species shown in Tab. 1. Methods for scanning electron microscopy (SEM) were as previously described (Kosuge & Tamura 1988).

Observations At the base of a dome-shaped floral apex, sepal primordia are produced spirally. Shortly after the inception of the last sepal primordium, petal and stamen primordia arise centripetally and spirally, except in *Aquilegia* where they are arranged in cyclic pattern. The sepal primordia are more or less flat at first and soon they cover the floral apex, while the petal primordia are nearly hemispherical like stamen's (Fig. 9) and are arranged on the staminal parastichies. In contrast to the stamen, petal primordia become enlarged and flat, but mostly its basal part is comparatively narrow in early stage and grows into a stalk later. Usually filaments elongate centrifugally but they elongate

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Tab. 1. The sources of the species examined.

<i>Trollius hondoensis</i> Nakai	Mt. Shirouma, Pref. Niigata
<i>Anemonopsis macrophylla</i> Sieb. & Zucc.	Cult. at the Botanic Garden, Nikko, Tokyo University
<i>Cimicifuga japonica</i> (Thunb.) Spreng.	Mt. Kuju, Pref. Oita
<i>Eranthis pinnatifida</i> Maxim.	Mt. Ibuki, Pref. Shiga
<i>Helleborus orientalis</i> Lam.	Cult. at Kobe University
<i>Delphinium grandiflorum</i> L.	Cult. at the Botanic Garden, Berlin-Dahlem
<i>Consolida ajacis</i> L.	Cult. at Kobe University
<i>Adonis amurensis</i> Regel & Radde	Mt. Fujiwara, Pref. Mie
<i>Ranunculus silerifolius</i> Lév.	Mt. Kongo, Pref. Osaka
<i>R. sceleratus</i> L.	Nagaokakyo, Pref. Kyoto
<i>Dichocarpum pterigionocaudatum</i> (Koidz.) Tamura & Lauener	Mt. Hunakoshi, Pref. Hyogo
<i>D. dicarpon</i> (Miq.) W. T. Wang & Hsiao	Mt. Kuju, Pref. Oita
<i>D. nipponicum</i> (Franch.) W. T. Wang & Hsiao	Mt. Yudono, Pref. Yamagata
<i>Isopyrum thalictroides</i> L.	Cult. at the Botanic Garden, Berlin-Dahlem
<i>Semiaquilegia adoxoides</i> (DC.) Makino	Mt. Koya, Pref. Nara
<i>Aquilegia buergeriana</i> Sieb. & Zucc.	Mt. Koya, Pref. Nara
<i>Coptis quinquefolia</i> Miq.	Mt. Hira, Pref. Shiga
<i>C. japonica</i> var. <i>dissecta</i> (Yatabe) Nakai	Mt. Koya, Pref. Nara
<i>Xanthorrhiza simplicissima</i> Marshall	Cult. at the Botanic Garden, Nikko, Tokyo University

centripetally in *Anemonopsis*, *Trollius*, *Delphinium* and *Consolida*. The petals grow after the elongation of the outermost stamens (Fig. 22), except in *Cimicifuga* and *Anemonopsis* (Fig. 3). The petals expand quickly just before or during anthesis and are usually shorter than sepals except in *Adonis* and *Ranunculus*.

In the following section, petals are described after hemispherical primordia become flat.

Trollius hondoensis. The number of primordia is 13-18. The basal part is somewhat narrow and develops into a claw later. The upper part of primordia becomes slightly depressed (Fig. 1), the lower edge of depression becomes a little thick and the upper blade recurves at anthesis.

Anemonopsis macrophylla. The number of primordia is 10-11. The median basal part is thick on both sides along a mid-vein (Fig. 2), but the adaxial thickening becomes gradually unclear. Petals are flat without a nectary.

Cimicifuga japonica. The number of primordia is 1-2. They become concave, covering stamens just like sepals. A transverse ridge appears near the base of petal and both ends do not extend to the lateral margins of the blade (Fig. 4). Petals become slightly depressed above the ridge and short clawed. A nectary appears in the depression.

Eranthis pinnatifida. The number of primordia is 5-7. The upper part becomes expanded and slightly depressed. The upper margin of the abaxial wall is two lobed and two bulges arise at the lower edge of the depression (Fig. 5). The edge grows to form the wall on the adaxial side. At the middle part of the adaxial wall, between two bulges, the growth is retarded, as a result of which the adaxial wall becomes two-lobed. Through the growth of both adaxial and abaxial walls, the limb becomes tubular at the base (Fig. 6). The stalk is shorter than the limb.

Helleborus orientalis. The number of primordia is 10-15 and in the early stage, the development of primordia resembles that of *Eranthis*, but the growth of the adaxial wall is slightly retarded at the middle. Thus, the upper margin of the adaxial wall is not obviously two-lobed and the limb becomes distinctly tubular.

Delphinium grandiflorum. The number of primordia is 8 and become continuous slightly at the base. The lower four primordia cease growing (Fig. 7) or sometimes grow into staminodes. In the upper four primordia, the dorsal two become depressed to form the spur and the depressions are shifted proximally (Fig. 7). Two petals are pressed to each other and the walls between the spurs are absent (Fig. 8). During the spur elongation, the lower edge of the spur mouth becomes ridged. The proximal ends of ridges are pressed to each other and the distal ends do not extend to the petaline margin. The lateral petals are not depressed and are thick at the base (Fig. 7). The thickening grows into U-shaped ridge whose lateral arms elongate upward along both lateral veins.

Consolida ajacis. The number of primordia is 8 but sometimes the lower primordia are not developed. The basal part becomes continuous, especially in the dorsal two (Fig. 9). The two primordia grow forming a single petal. The petal is bi-lobed at the apex (Fig. 10) and two lobes correspond to two

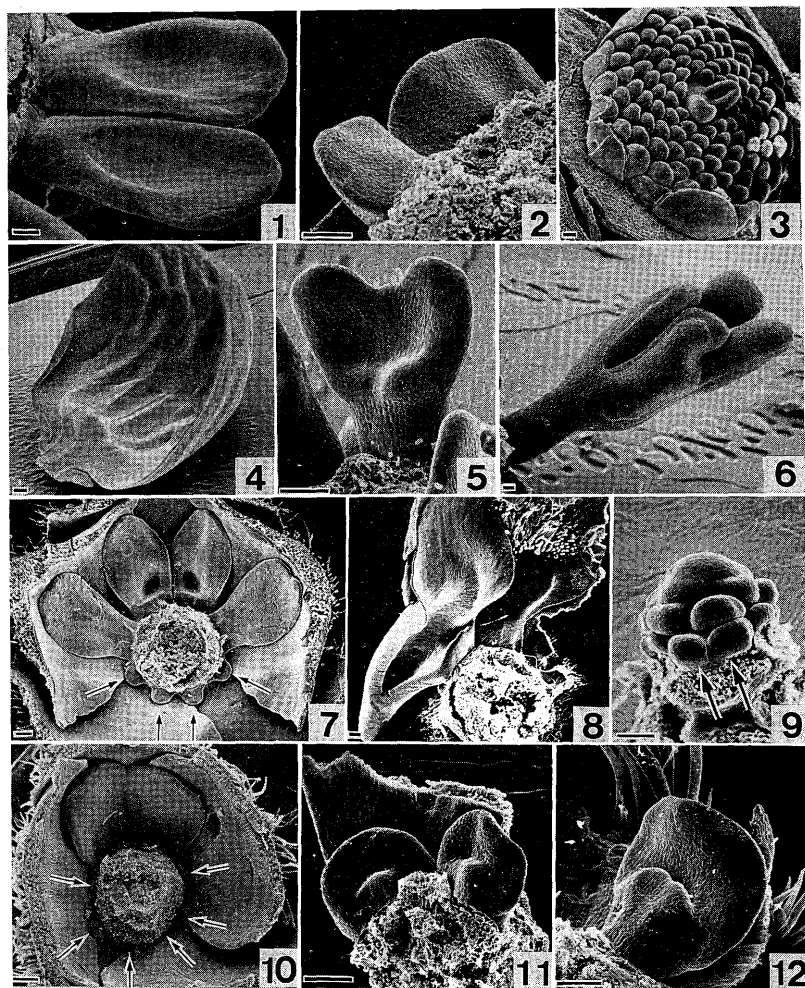


Fig. 1. *Trollius hondoensis*. Slightly depressed petals. Figs. 2-3. *Anemonopsis macrophylla*. 2: Petals thick on both sides along the mid-vein. 3: Petals and stamens elongate centripetally. Fig. 4. *Cimicifuga japonica*. Transverse ridge near the base of petal. Figs. 5-6. *Eranthis pinnatifida*. 5: Two bulges at the lower edge of the depression. 6: Slightly tubular at the base and four-lobed petal. Figs. 7-8. *Delphinium grandiflorum*. 7: Lower four primordia (arrows) cease growing, the dorsal two depressed, but the lateral two are not depressed. 8: Spur wall absent between dorsal two petals. Figs. 9-10. *Consolida ajacis*. Petal primordia resemble stamen primordia, the dorsal two (arrows) continuous at the base. 10: The dorsal two primordia form a single petal but 6 others (arrows) cease growing. Figs. 11-12. *Ranunculus silerifolius*. 11: Bulge at the middle of petal. 12: Petals with the adaxial scale. Bar=0.1 mm.

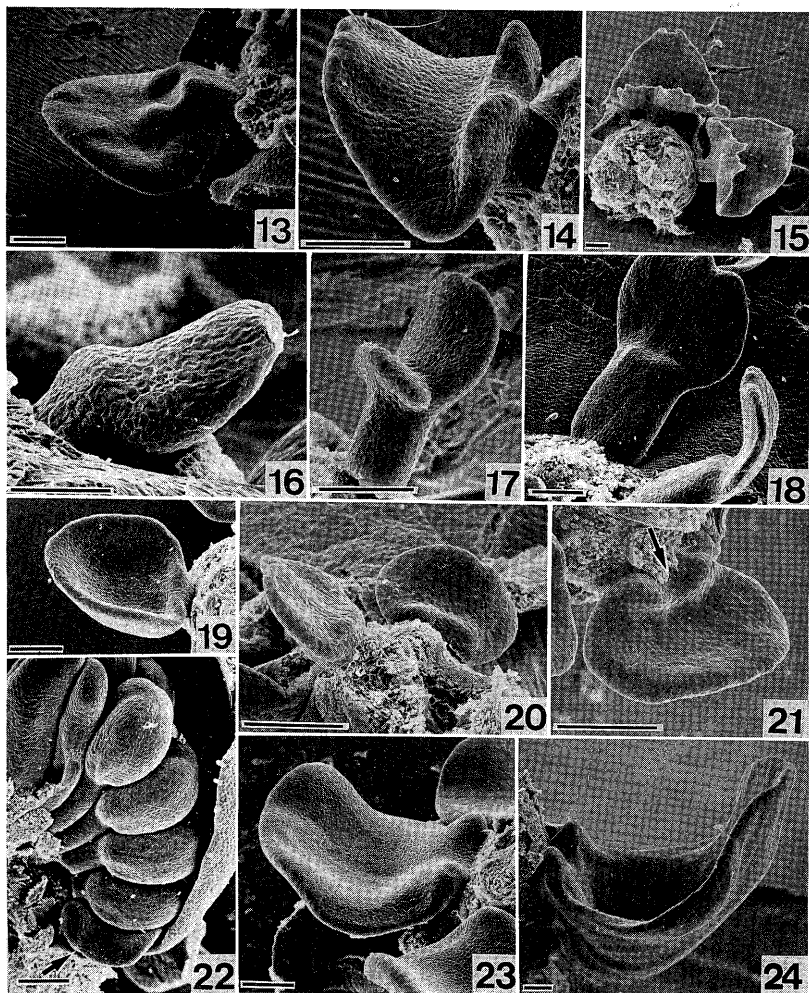
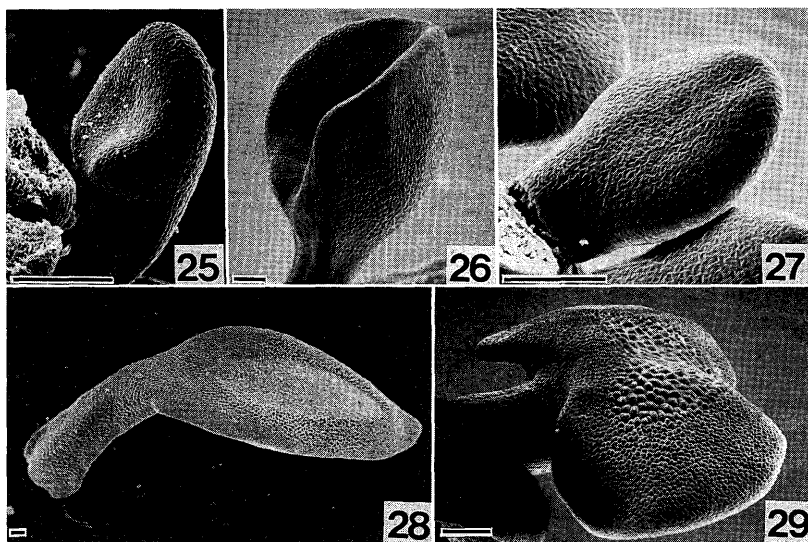


Fig. 13. *Ranunculus sceleratus*. 13: Horseshoe-shaped ridge at the middle of petal. Figs. 14-15. *Dichocarpum pterigionocaudatum*. 15: Two bulges at the lower margin of the limb. 16: Two bulges become obscure. Figs. 17-18. *D. dicarpon*. 17: Transverse ridge at the lower edge of the limb. 18: Adaxial labium perpendicular to the abaxial one. Fig. 19. *D. nipponicum*. Ridge ceases growing and remains as a thickening. Fig. 19. *Isopyrum thalictroides*. Thickening along the lower edge of the limb. Figs. 20-21. *Semiaquilegia adoxoides*. 20: Transverse ridge at the base of petal. 21: Petal depressed above the ridge and the adaxial wall concaved at the middle (arrow). Figs. 22-24. *Aquilegia buergeriana*. 22: Petal (arrow) and filaments elongate centrifugally. 23: Two bulges arise at the base of petal. 24: Adaxial wall between two bulges slightly developed. Bar=0.1mm.



Figs. 25-26. *Coptis quinquefolia*. 25: The limb is depressed at the center. 26: The limb is shallow, thick and cup-shaped. Figs. 27-28. *C. japonica*. 27: Flat petal. 28: Nectariferous tissue differentiated on the adaxial surface. Fig. 29. *Xanthorhiza simplicissima*. The limb is curved downward and nectariferous tissue is differentiated on the adaxial side. Bar=0.1 mm.

primordia. Other primordia cease the growth in early stage. The petal is depressed near the base as forming the spur and the ridge develops like *Delphinium*.

Adonis amurensis. The number of primordia is 15-20 and their development resembles that of *Anemonopsis*. However, petals grow slower than stamens and the thickening on the abaxial side is not observed. Petals are completely flat without a nectary.

Ranunculus silerifolius. The number of primordia is 5. A bulge develops at the middle on the adaxial side (Fig. 11) and grows to an adaxial scale (Fig. 12). This scale does not extend to the main blade margin. Compared with the petal at anthesis, the relative size of the scale to the blade is much larger in younger petal. The blade elongates rapidly and the adaxial scale covering a nectary remains at the base.

R. sceleratus. The early development roughly resembles that of *R. silerifolius*. But the basal part of primordia grows to a short stalk and the bulge becomes a horseshoe-shaped ridge (Fig. 13). This shape either remains unchanged or sometimes both ends of the ridge are connected to form a continuous border

surrounding a nectary. Rarely, the ridge does not surround the nectary and its lower part projects slightly downward.

Dichocarpum pterigionocaudatum. The number of primordia is 5. The upper part becomes expanded and slightly depressed. Two bulges arise at the lower edge of the depression, i.e., at the lower margin of the limb (Fig. 14). Later, these two bulges become obscure by the growth of the adaxial wall between them (Fig. 15). The limb becomes cup-shaped and is shorter than the stalk at anthesis.

D. dicarpon. The early development is roughly similar to that of the preceding species but a transverse ridge appears instead of two bulges (Fig. 16). The ridge extends to the limb margin and grows to the adaxial labium perpendicular to the abaxial one (Fig. 17). The wall of the limb is not developed at both lateral sides and the limb becomes bi-labial. A nectary is differentiated at the base between two labia and the stalk bent at the top, then the limb is hanging down inside.

D. nipponicum. The early development is roughly similar to that of *D. dicarpon*, but a transverse ridge ceases the growth and remains as a thickening (Fig. 18). Hence, the limb is uni-labial and a nectary present above the thickening.

Isopyrum thalictroides. The number of primordia is 5. The upper part becomes expanded, depressed and slightly thick along the lower edge of the depression, i.e., the lower margin of the limb (Fig. 19). The limb becomes obliquely cup-shaped through the unequal growth, i.e., the abaxial wall is much more enlarged than the adaxial one and hollowed near the base of the limb. The basal part grows to a short stalk.

Semiaquilegia adoxoides. The number of primordia is 5. The upper part becomes expanded and a transverse ridge arises at the base. The ends of the ridge do not extend to the lateral margins of petal at first (Fig. 20), but they do so later. The ridge is concave at the middle where the filament is pressed. The limb becomes depressed above the ridge (Fig. 21) and the depression develops into a short spur. Petal becomes slightly tubular through the growth of the ridge and abaxial wall. The basal part converts into a short, thick stalk.

Aquilegia buergeriana. The number of primordia is 5. The early development of primordia resembles that of *D. pterigionocaudatum* (Fig. 23). However, the adaxial wall between two bulges is only slightly developed while the stalk

is not developed (Fig. 24). The abaxial wall is enlarged much more than the adaxial side and remarkably depressed as to form a long spur.

Coptis quinquefolia. The number of primordia is 5. The upper part of primordia is expanded, thickened and depressed at the center (Fig. 25). The margin of the depression is raised and the limb becomes shallow, thick and cup-shaped (Fig. 26). The basal part grows to the stalk, which is longer than the limb.

C. japonica var. *dissecta*. The number of primordia is 9-11. The upper expanded part of primordia is not depressed, and its narrow basal part develops into a stalk (Fig. 27). Nectariferous tissue is differentiated on the adaxial surface, except for marginal part (Fig. 28).

Xanthorhiza simplicissima. The number of primordia is 5. The upper part is thick, enlarged and the adaxial side turns upside. Nectariferous tissue is differentiated on the adaxial surface, similar to the preceeding species, and the limb is curved downward at first (Fig. 29), which becomes depressed at the center at anthesis.

Discussion In the nectariferous petals, hemispherical primordia become flat, depressed and the adaxial appendage arises at the lower edge of the depression, then the limb becomes tubular or spurred. In the tubular or cup-shaped petal usually the stalk is long and the margin of the depression of petal corresponds to that of the limb. Thus, the adaxial appendage develops into the adaxial wall of the limb. The petals of *Dichocarpum* are long stalked and vary from tubular to flat. The petal with tubular limb is found in *D. pterigionocaudatum*. In *D. dicarpon* var. *decumbens*, they are slightly cup-shaped, though the wall of cup is short at both lateral sides. In flat petals of *D. nipponicum*, the adaxial ridge develops like bi-labial ones of *D. dicarpon* var. *dicarpon* at first, but cease growing later. Accordingly, the cup-shaped limb may become bi-labial by the reduction of the wall at the lateral sides, then become flat by the reduction of the adaxial wall. In *Isopyrum* and *Semiaquilegia*, the petals are tubular, slightly hollowed or spurred and short stalked, while in *Aquilegia*, the petals are somewhat tubular with short adaxial wall, long spur and sessile. In both types of petals, it seems that the more the spur develops, the more the adaxial wall and the stalk are reduced. The long spurred petals are also observed in trib. Delphinieae. In *Aconitum* they are sometimes tubular with grooved stalks (Kosuge & Tamura 1988). While in *Delphinium* and *Consolida*, the petals are not tubular and sessile, and their

adaxial wall is short. Therefore the stalk becomes short, flat and undistinguishable from the blade.

The nectariferous petals are usually depressed in early stage, but in *Xanthorhiza* they are depressed not in early stage but at anthesis, and in *Coptis japonica* they are never depressed. In *Ranunculus* they enlarge, replace sepals and are not depressed. The petals of *Cimicifuga japonica* are large, caducous like sepals, grow faster than stamens and are not depressed in early stage. In some species of *Cimicifuga* the petals are nectarless but in *C. japonica* they produce small amount of nectar and seem to be in the transitional state of the nectary reduction.

The nectarless petals of *Anemonopsis* and *Adonis* are completely flat without the adaxial appendage and depression through the process of development.

The course of petal evolution was already shown by Schrödinger (1909), Tamura (1965), Hiepko (1965) and others. According to these investigators, petals are originally peltate with a short limb and a long stalk. The present studies, however, do not show clearly whether petals are peltate in origin. The adaxial appendage arises later on the abaxial blade in contrast to the peltate carpel. But as in young petals of *Ranunculus*, the relative size of the adaxial appendage is larger than that of the abaxial blade. In *Eranthis*, *Dichocarpum pterigionocaudatum* and *Aquilegia*, the adaxial appendage arises as two bulges, which seems to be due to the filament of the stamen pressing the middle of the adaxial wall. In the early stage of development, petal primordia are similar to stamen primordia and in *Coptis quinquefolia* petals resemble stamens in the adult stage. If we presume that the cup-shaped, long stalked and nectariferous petals, as in *C. quinquefolia*, are the original petal type, the spurred ones or flat petaloid ones are the transformed types derived by the reduction of the stalk and adaxial wall. Furthermore, they become flat by the loss of the nectar secretion. In *Delphinium* two primordia form two petals pressed against each other while in *Consolida* two primordia form a single petal.

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キンボウゲ科において花卉は雄しべが変化したもので楯型器官とみなされているが、心皮で報告されているような発生段階の観察は行なわれていない。従って、今回、19種で花卉の発生過程を走査型電子顕微鏡により観察した。花卉原基は雄しべ原基に似ているが、平たくなり、向軸側の構造は遅れて現れ、楯型の心皮の発生とは異なる。向軸側中央部の成長はしばしば雄しべの花糸により抑制され、セツブンソウやオダマキでは両側の2個の膨らみとして現れる。多くの場合、平たくなった原基の中央部はくぼみ、向軸側の壁が現れ、蜜腺が分化し、柄は遅れて伸長する。*Delphinium* やオダマキでくぼみはさらに発達し、距を形成するが、一方、キンボウゲ属では花卉はくぼまず、がくより大きくなる。このような花卉では向軸側の壁や柄はあまり発達しない。蜜を分泌しないレンゲショウマやフクジュソウの花弁は平たく、くぼみや向軸側の構造は生じない。バイカオウレンの花弁は蜜を分泌し、舷部がコップ状で長い枝があり、雄しべによく似ている。これを花卉の原型とすると、距や花卉状のものは向軸側の構造と枝の退化によって生じ、さらに蜜腺の退化により、平たい花卉が生じたと思われる。